The integration of three-dimensional Lotka–Volterra systems

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The general solutions of many three-dimensional Lotka–Volterra systems, previously known to be at least partially integrable, are constructed with the aid of special functions. Examples include certain ABC and May–Leonard systems. The special functions used are incomplete beta and elliptic functions. In some cases the solution is parametric, with the independent and dependent variables expressed as functions of a 'new time' variable. This auxiliary variable satisfies a nonlinear third-order differential equation of a generalized Schwarzian type, and results of Carton-LeBrun on such equations are exploited. Several difficult Lotka–Volterra systems are successfully integrated in terms of Painlevé transcendents. An appendix on incomplete beta functions is included.

Key words: Lotka–Volterra system; generalized Schwarzian equation; Painlevé property.

1. Introduction

(*a*) *Background*

Models of Lotka–Volterra type occur frequently in the physical and engineering sciences, as well as the biological. In any such model there is a d-dimensional state vector $x = (x_1, \ldots, x_d)$, a function of time τ, which satisfies an autonomous system of ordinary differential equations (ODE's) of the form

$$\dot{x}_i = x_i\left(a_{i0} + \sum_{j=1}^{d} a_{ij}x_j\right), \qquad i = 1, \ldots, d. \tag{1.1}$$

The overdot signifies $\mathrm{d}/\mathrm{d}\tau$. By letting $x_0 \equiv 1$ and $a_{0i} \equiv 0$ one can optionally rewrite this as $\dot{x}_i = x_i \sum_{j=0}^{d} a_{ij}x_j$, $i = 0, \ldots, d$. There is a paucity of closed-form solutions: when $d \geqslant 3$ and even when $d = 2$, the system (1.1) is usually integrated numerically rather than symbolically.

In most applications $x_i \geqslant 0$ for all i, though it may be useful to allow the x_i and even τ to be complex. Such models were first introduced in population ecology (Kot 2001; May 2001), where x lies in the non-negative orthant, and the terminology reflects this: a_{i0} is the growth rate of the i'th 'species,' and depending on the signs of the elements of the interaction matrix $\mathsf{A} = (a_{ij})_{i,j=1}^{d}$, one speaks of predation, competition or mutualism. If $a_{i0} > 0$ and $a_{ii} < 0$, in the absence of

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the other $d-1$ species the i'th species will grow logistically, but the behaviour of $x=x(\tau)$ in the interior of the orthant may be much more complicated.

Modelling by small-d Lotka–Volterra systems has occurred many times in physics. In laser physics this ranges from the initial treatment of multimode coupling (Lamb 1964) to Raman amplification in an optical fibre (Castella et al. 2008), where τ is the distance along the fibre. Other physical applications include the modelling of the (integrable) interaction of Langmuir waves in plasmas (Qin et al. 2011) and more chaotic phenomena: the Kueppers–Lortz instability in a rotating fluid (Busse 1983; San Miguel & Toral 2000), for which $d=3$, and the Boltzmann dynamics of d rarefied, spatially homogeneous gases in a background medium (Jenks 1969; Lupini & Spiga 1988). Several integrable Lotka–Volterra systems with fairly small d, of mathematical interest, have been obtained as spatial discretizations of the Korteweg–de Vries equation, or as generalizations of same (Bogoyavlensky 1988; Bogoyavlenskij 2008).

In population biology, small-d Lotka–Volterra systems include the classical $d=2$ predator–prey model of Volterra and Lotka, well-known though structurally unstable; the famous May–Leonard model of $d=3$ cyclically competing species with equal growth rates, which has a stable limit cycle (May & Leonard 1975); and generalizations that model the asymmetric competition of d species in a chemostat (Wolkowicz 2006; Ajbar & Alhumaizi 2012). There is also a literature on evolutionarily stable strategies in game dynamics, modelled by differential systems equivalent to Lotka–Volterra ones (Hofbauer & Sigmund 1988, 2003). Lotka–Volterra systems with $d\geqslant 3$ may display chaotic behaviour, a fact first noted in ecological modelling (Klebanoff & Hastings 1994; Vano et al. 2006).

Many nonquadratic nonlinear differential systems can be transformed to (1.1) by changes of variable (Peschel & Mende 1986; Brenig & Goriely 1989; Gouzé 1992; Hernández-Bermejo & Fairén 1997). Complex chemical reactions with mass-action kinetics provide examples. For special stoichiometries, spatially homogeneous species concentrations evolve in a Lotka–Volterra way (Érdi & Tóth 1989; Murza & Teruel 2010). Furthermore, mass-action systems with nonquadratic polynomial nonlinearities, which can be obtained from (formal) chemical reactions in more than one way, can often be transformed to the Lotka–Volterra form.

Several elementary changes of variable deserve mention, for any d-dimensional system of the form (1.1). First, by scaling τ one can scale the column vector of growth rates and the interaction matrix A. Additionally, by scaling $x_1,\dots,x_d$ independently one can scale independently the d columns of A. Thus the parameter space has dimensionality not d^2+d but d^2-1.

If the growth rates $a_{10},\dots,a_{d0}$ are *equal* (to a_{*0}, say), then in terms of a transformed time $\tau' := \mathrm{e}^{a_{*0}\tau}$ the transformed variables $x'_i := \mathrm{e}^{-a_{*0}\tau}x_i$ will satisfy a system of the form (1.1) but with zero growth rates. Furthermore (Plank 1999), if $x_1,\dots,x_d$ satisfy (1.1) with zero growth rates then the ratios $(\tilde{x}_1,\dots,\tilde{x}_{d-1}) := (x_1/x_d,\dots,x_{d-1}/x_d)$ will satisfy a $(d-1)$-dimensional system resembling (1.1), but with growth rates $\tilde{a}_{i0} := a_{id}-a_{dd}$ and interactions $\tilde{a}_{ij} := a_{ij}-a_{dj}$. Thus Lotka–Volterra systems with equal growth rates, for which the parameter space dimensionality is effectively d^2-d, should be peculiarly amenable to analysis; though even they have usually been studied not symbolically but numerically.

The object of this paper is the construction of general solutions $x = x(\tau)$ of systems of the form (1.1), with the aid of special functions. The focus is on $d = 3$ systems, though ancillary results on integrable $d = 2$ systems are obtained first. The special functions employed are the incomplete beta function and its inverse, which sometimes reduces to an elementary or elliptic function. For many $d = 3$ systems known to be at least partially integrable, general solutions are constructed for the first time, with unexpected ease. By default, each of x, τ is expressed as a function of an auxiliary variable t, a 'new time.' A minor but interesting example is the fully (rather than merely cyclically) symmetric May–Leonard model.

Most of the integrated systems have equal growth rates, but not all. Several systems with unequal ones which have the Painlevé property, that each solution $x = x(\tau)$ can be extended analytically to a one-valued function on the complex τ-plane, are integrated with the aid of Painlevé transcendents.

Many of the interesting examples of general solutions $x = x(\tau)$ that are presented are made possible by results of Carton-LeBrun (1969). She classified all nonlinear third-order ODE's of a certain type that have the Painlevé property; and the ODE satisfied by the new time $t = t(\tau)$ used here was fortuitously included. She also integrated many such ODE's with the aid of elliptic functions. The examples in §§ 3 and 4 may serve to reawaken interest in her work.

This paper includes an appendix on closed-form expressions for inverse incomplete beta functions, which should be of independent interest.

(*b*) *Previous results, reformulated*

The following is a summary of symbolic (non-numerical) results on small-d Lotka–Volterra systems, which provides the context for the new results.

Lotka–Volterra solutions cannot always be expressed in closed form, i.e. in terms of elementary or 'known' functions, even if the behaviour of the solutions is nonchaotic; or so it is believed. An example is the original system of Volterra and Lotka, with $d = 2$ and no self-interactions ($a_{11} = a_{22} = 0$). If the growth rates are equal it has a general solution in terms of elementary functions (Varma 1977). If the rates are unequal it is nonetheless integrable (see below) and hence nonchaotic, but this does not imply the existence of a useful closed form for the general solution. The case of unequal growth rates when $d = 2$ has in fact been used as a test-bed for geometric numerical integration schemes (Hairer et al. 2006).

Owing to the difficulty of constructing explicit solutions of systems of the form (1.1), there has been much work on the simpler problem of finding constants of the motion, i.e., first integrals. Any such is a function $I = I(x_1, \ldots, x_d)$, preferably one-valued and well-behaved, obeying $\dot{I} = 0$ on any system trajectory. (By the overdot the total time derivative is meant.) If such an I exists, any trajectory is confined to a $(d-1)$-dimensional surface $I \equiv \text{const}$; which, e.g., facilitates the study of long-time behaviour. If there are $d - m$ functionally independent first integrals then motion is confined to a m-dimensional surface, obtained as an intersection. When $m = 1$ the system is completely integrable (its general solution can be 'reduced to quadratures,' though not necessarily usefully). When $m = 2$ it is partially integrable and is at least nonchaotic.

For $d = 2, 3$, restrictions on the Lotka–Volterra parameters $\{a_{ij}\}_{i=1,j=0}^{d}$ that imply the existence of a single closed-form first integral have been investigated by

many authors. In most cases the resulting first integral is of the form

$$I = \prod_{k=1}^{r} |f_k|^{l_k}\,, \tag{1.2}$$

with each $f_k = f_k(x_1, \ldots, x_d)$ a polynomial (usually though not always of degree 1 with constant term allowed). Results along this line include those of Cairó and collaborators (Cairó & Feix 1992; Cairó et al. 1999; Cairó 2000; Cairó & Llibre 2000), who in many cases used the classical technique of Darboux polynomials (Goriely 2001); and results based on an integrating factor technique (Saputra et al. 2010). When $d=3$ and a single first integral of a form similar to (1.2) exists, there has been some work on the construction of a second, functionally independent first integral of a more complicated and less algebraic form (Grammaticos et al. 1990; Goriely 1992; Gao 2000; Bustamante & Hojman 2003).

The Darboux polynomial (DP) concept is fundamental. A DP $f = f(x_1, \ldots, x_d)$ is a polynomial for which $\dot{f} = Kf$ along any system trajectory, where the 'cofactor' $K = K(x_1, \ldots, x_d)$ is necessarily also a polynomial, of degree 1 with constant term allowed. The algebraic surface $f = 0$ is thus invariant under the Lotka–Volterra flow. If the cofactors of DP's $f_1, \ldots f_r$ are linearly dependent, some product of the form (1.2) will be a first integral: generically, a non-trivial one. Finding a first integral, including the needed parametric restrictions, is facilitated by the coordinate functions $x_1, \ldots, x_d$ being DP's, associated to the invariant hyperplanes $x_i = 0$, $i = 1, \ldots, d$, and having respective cofactors $K_i = \sum_{j=0}^{d} a_{ij}x_j$. To construct a first integral a single additional DP f will suffice, if one sufficiently restricts parameters to ensure dependence of the cofactors of $x_1, \ldots, x_d, f$.

Tables 1 and 2 are a distillation of the results of the preceding authors on degree-1 DP's f that yield first integrals of the form $|x_1|^{l_1} \ldots |x_d|^{l_d}\,|f|^{l_{d+1}}$. In the two tables, i, j and i, j, k are arbitrary permutations of $1, 2$ and $1, 2, 3$, respectively; and $f = 0$ is an invariant line, resp. plane. For both $d = 2$ and 3, the cases when $\leqslant d$ restrictions on the parameters yield a first integral of this form split into three types: I, II and III. (The numbering here differs from that of Cairó & Feix (1992) but agrees with that of Hua et al. (1996).) The primed cases can be viewed as projectively transformed versions of the unprimed ones. For instance, the $d = 2$ case II'_i is related to II by $(\tilde{x}_0, \tilde{x}_i, \tilde{x}_j) = (x_j, x_i, x_0)/x_j$.

The type-I cases are degenerate: the first integral I does not require any additional DP f and is merely of the form $\prod_{i=1}^{d} |x_i|^{l_i}$. In fact, in each type-I case the restrictions on the parameters, expressed in terms of the $d+1$ column vectors $a_j := (a_{ij})_{i=1}^{d}$, $j = 0, \ldots, d$, imply that the matrix $\mathsf{A} = (a_{ij})_{i=1,j=1}^{d}$ must be singular, i.e., $\det \mathsf{A} = 0$. Lotka–Volterra models with singular A (e.g., ones in which A is antisymmetric and d is odd) may have physical applications, though their relevance to population ecology has been strongly questioned (Maynard Smith 1974; May 2001). But they will not be considered further here.

For $d = 2$, in case II (which is defined by $a_{10} = a_{20} = 0$, i.e., by the growth rates of the two species being zero), the resulting first integral is easily seen to be

$$I = |x_1|^{a_{22}(a_{21}-a_{11})}\,|x_2|^{a_{11}(a_{12}-a_{22})}\,|(a_{11}-a_{21})x_1 - (a_{22}-a_{12})x_2|^{\Delta}\,, \tag{1.3}$$

where $\Delta := \det \mathsf{A}$. For $d = 3$, the similar case II_i is defined by $a_{j0} = a_{k0} =: a_{*0}$, i.e., by the two species other than species i having equal growth rates, and by

Table 1. For $d=2$, cases when $\leqslant 2$ restrictions yield a Darboux polynomial f and a first integral: $|x_1|^{l_1}\,|x_2|^{l_2}\,|f|^{l_3}$.

case	restrictions	DP f	cofactor of f
I	$\det(a_0,a_2)=\det(a_1,a_0)=0$	none needed	—
I'_i	$\det(a_i,a_j)=\det(a_0,a_i)=0$	none needed	—
II	$a_{10}=a_{20}=0$	$(a_{11}-a_{21})x_1-(a_{22}-a_{12})x_2$	$a_{11}\,x_1+a_{22}\,x_2$
II'_i	$a_{ij}=a_{jj}=0$	$a_{i0}+a_{ii}\,x_i$	$a_{ii}\,x_i$
III	$r_{012}=0$	$a_{10}a_{20}+a_{20}a_{11}\,x_1+a_{10}a_{22}\,x_2$	$a_{11}\,x_1+a_{22}\,x_2$

Table 2. For $d=3$, cases when $\leqslant 3$ restrictions yield a Darboux polynomial f and a first integral: $|x_1|^{l_1}\,|x_2|^{l_2}\,|x_3|^{l_3}\,|f|^{l_4}$.

case	restrictions	DP f	cofactor of f
I	$\det(a_0,a_2,a_3)=\det(a_1,a_0,a_3)$ $=\det(a_1,a_2,a_0)=0$	none needed	—
I'_i	$\det(a_i,a_j,a_k)=\det(a_0,a_i,a_k)$ $=\det(a_0,a_j,a_i)=0$	none needed	—
II_i	$a_{j0}=a_{k0}=: a_{*0}$, $a_{ji}=a_{ki}=: a_{*i}$, $a_{i0}a_{*i}=a_{*0}a_{ii}$	$(a_{jj}-a_{kj})x_j-(a_{kk}-a_{jk})x_k$	$a_{*0}+a_{*i}\,x_i+a_{jj}\,x_j+a_{kk}\,x_k$
II'_i	$a_{ij}=a_{ik}=0$, $a_{jj}a_{kk}=a_{jk}a_{kj}$	$a_{i0}+a_{ii}\,x_i$	$a_{ii}\,x_i$
III_i	$r_{0jk}=0,\ a_{ji}=a_{ki}=0$	$a_{j0}a_{k0}+a_{k0}a_{jj}\,x_j+a_{j0}a_{kk}\,x_k$	$a_{jj}\,x_j+a_{kk}\,x_k$
III'	$r_{123}=0,\ a_{10}=a_{20}=a_{30}=: a_{*0}$	$(a_{ji}-a_{ii})(a_{ki}-a_{ii})x_i$ $-(a_{ij}-a_{jj})(a_{ki}-a_{ii})x_j$ $-(a_{ik}-a_{kk})(a_{ji}-a_{ii})x_k$	$a_{*0}+a_{11}\,x_1+a_{22}\,x_2+a_{33}\,x_3$

$a_{ji} = a_{ki} =: a_{*i}$, i.e., by their having equal effects on species i. A third condition $a_{i0}a_{*i} = a_{*0}a_{ii}$ must also be satisfied. (Note that it will be satisfied if all growth rates are zero.) The resulting first integral is

$$I = |x_i|^{a_{*i}(a_{kj}-a_{jj})(a_{jk}-a_{kk})}\ |x_j|^{(a_{ii}a_{kk}-a_{ik}a_{ki})(a_{kj}-a_{jj})}\ |x_k|^{(a_{ii}a_{jj}-a_{ij}a_{ji})(a_{jk}-a_{kk})} \times |(a_{jj}-a_{kj})x_j - (a_{kk}-a_{jk})x_k|^{\Delta}. \quad (1.4)$$

The $d=3$ expression (1.4) reduces to a power of the $d=2$ first integral (1.3) when $(i,j,k) = (3,1,2)$ and the third species decouples: $a_{*i} = 0$.

The tables also list restrictions of type III, which are expressed in terms of the quantities

$$r_{ijk} := (a_{ji}-a_{ii})(a_{kj}-a_{jj})(a_{ik}-a_{kk}) + (a_{ki}-a_{ii})(a_{ij}-a_{jj})(a_{jk}-a_{kk}). \quad (1.5)$$

But the present paper will focus entirely on $d=2$ and especially $d=3$ systems that satisfy the less complicated restrictions of type II, resp. type II_i.

It must be stressed that Lotka–Volterra systems with $d=2,3$ and no self-interactions ($a_{ii}=0$ for $i=1,\dots,d$) do not fit well into the DP framework of tables 1 and 2. One example is the classical $d=2$ model, which has the two restrictions $a_{11}=a_{22}=0$ and is quite anomalous. It is integrable with first integral

$$I = |x_1|^{a_{20}}\,|x_2|^{-a_{10}}\,[\exp(a_{21}x_1 - a_{12}x_2)] =: \prod_{i=1}^{3} |f_i|^{l_i}. \quad (1.6)$$

A framework into which this model fits is only now being developed (Llibre & Zhang 2009). Each factor f_i in (1.6) satisfies $\dot{f}_i = K_i f_i$ for some degree-1 polynomial cofactor K_i and is therefore a DP or generalized DP, sometimes called a 'second integral' (Goriely 2001). To understand (1.6) one needs the concept of the *multiplicity* of an invariant line (or algebraic curve) of a polynomial vector field (Christopher et al. 2007). The DP's $f_1 = x_1$, $f_2 = x_2$ are associated to the invariant lines $x_1 = 0$, $x_2 = 0$, which by default are not multiple. The exponential factor f_3 in (1.6) comes from the line 'at infinity,' which like $x_1 = 0$ and $x_2 = 0$ is invariant in any Lotka–Volterra model but which when $a_{11} = a_{22} = 0$ has a nontrivial (double) multiplicity. It therefore gives rise to an extra (generalized) DP, namely f_3.

The extent to which imposing parametric restrictions on a $d=2$ Lotka–Volterra system can produce single or multiple invariant lines, thereby engendering DP's or generalized DP's, is now fully understood (Schlomiuk & Vulpe 2010). The number of invariant lines, counted with multiplicity, can if finite be as large as six (including the one at infinity). The line configuration 4.18 of Schlomiuk & Vulpe corresponds to the classical model ($a_{11} = a_{22} = 0$), and their 4.5 and 4.1 to the types II and III of table 1. But an integrability study of their many other configurations, most defined by severe parametric restrictions and many including multiple invariant lines, remains to be carried out. A $d=3$ counterpart to their $d=2$ analysis, which is lengthy, is not yet available. The many possible configurations of invariant planes have not been fully classified, though partial results have been obtained (Cairó 2000; Saputra et al. 2010).

There is already a large literature on the integrability properties of $d=3$ Lotka–Volterra systems without self-interactions (Grammaticos et al. 1990; Cairó & Llibre 2000; Moulin Ollagnier 2001, 2004). They are called ABC or $A_1A_2A_3$ systems, since if $a_{11} = a_{22} = a_{33} = 0$ and $a_{ij}a_{jk}a_{ki} \neq 0$ for some

permutation ijk of 123, permuting species and scaling columns will yield an interaction matrix

$$\mathsf{A} = (a_{ij})_{i,j=1}^3 = \begin{pmatrix} 0 & A_2 & 1 \\ 1 & 0 & A_3 \\ A_1 & 1 & 0 \end{pmatrix}. \tag{1.7}$$

If an ABC system satisfies $A_1A_2A_3 = -1$ or $A_i = 1$ for some i, and growth rates are suitably constrained, a first integral for it can be constructed from degree-1 DP's. This is because such a system is of type I or type II, as defined in table 2. But there are exotic ABC systems with first integrals based on DP's of degree 2 or greater, or on generalized DP's. Being tightly restricted parametrically, they are not covered by table 2. Some of these systems were first obtained by a Painlevé analysis (Bountis et al. 1984). To some of these exotic ABC systems exotic $d = 2$ systems are associated, as any $d = 3$ system with equal growth rates can be reduced to a $d = 2$ system, typically with unequal growth rates (Cairó et al. 2003).

A $d = 3$ system with even tighter parametric restrictions is the May–Leonard model of cyclic competition (May & Leonard 1975). This is a system with equal growth rates (reducible to zero by a change of variables), and with

$$\mathsf{A} = (a_{ij})_{i,j=1}^3 = \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}. \tag{1.8}$$

If, e.g., $\alpha + \beta = -1$ or $\alpha = \beta = 1$, then $\det \mathsf{A} = 0$ and this system is of type I in the sense of table 2. If $\alpha = \beta$ (so that it is fully rather than cyclically symmetric), then it is of type II, and specifically it is case II_i for each i. Hence it is completely integrable: for each permutation ijk of 123, the expression (1.4) will be a first integral (cf. Strelcyn & Wojciechowski (1988)). Normalized, this is

$$I_i = |x_i|^{-\alpha}\, |x_j|^{\alpha+1}\, |x_k|^{\alpha+1}\, |x_j - x_k|^{-1-2\alpha}. \tag{1.9}$$

Other first integrals are known (Llibre & Valls 2011; Tudoran & Gîrban 2012).

The relation between the integrability (partial or complete) of a differential system and its having the Painlevé property (PP), i.e., the property that each of its solutions $x = x(\tau)$ has a one-valued continuation to the complex τ-plane (without branch points of any order), is a bit murky. It is widely believed that the integration of any system with the PP should reduce to quadratures; or if not, that the solutions of the system should be expressible in terms of 'known' functions, such as the Painlevé transcendents that arise as solutions of second-order ODE's with the PP. Like the $d = 3$ ABC system, the general $d = 2$ Lotka–Volterra system has been subjected to Painlevé analyses (Hua et al. 1996; Leach & Miritzis 2004). It appears that the only such systems with the PP also have DP's from which a first integral can be constructed; thus they are at least partially integrable. But a Painlevé analysis of general $d = 3$ Lotka–Volterra systems has yet to be performed. And until now, no explicit solution involving Painlevé transcendents of any $d = 3$ Lotka–Volterra system seems to have been published.

(c) *Overview of following results*

In § 2 we illustrate our methods by integrating the above case II of the $d = 2$ Lotka–Volterra system with the aid of a 'new time' t. The resulting expressions for x_1, x_2 and τ as functions of t, involving an incomplete beta function, are new.

This approach is equivalent to that of Goriely (1992), but unlike him we do not posit a fixed form for the new time transformation $t = t(\tau)$, or make explicit use of the first integral (1.3). Equal but nonzero growth rates are also treated.

In § 3 we obtain our central result: the general solution of case II_i of the $d = 3$ Lotka–Volterra system, initially requiring that the growth rates a_{10}, a_{20}, a_{30} be equal. Again the function $t = t(\tau)$ is not constrained *a priori*. It turns out to satisfy a generalized Schwarzian equation (gSE), which is integrated with the aid of the incomplete beta function. No explicit use is made of the first integral (1.4). Many systems are explicitly solved, including ABC and May–Leonard ones.

Section 3 relates our solution of case-II_i $d = 3$ systems to the results of Carton-LeBrun (1969), who classified all gSE's with the Painlevé property. Her results yield a classification of equal growth rate case-II_i systems with the property: each such has elementary or elliptic general solutions $x = x(\tau)$. In § 4 we express the general solutions of several $d = 3$ systems with unequal growth rates in terms of Painlevé transcendents. These may be the first such solutions ever obtained.

In § 5 we summarize the results of §§ 2–4, and make some final remarks.

2. Two-dimensional integration

To show how certain Lotka–Volterra systems of the form (1.1) can be integrated parametrically with the aid of a new time variable t, consider the case-II $d = 2$ systems of table 1: ones with $a_{10} = a_{20} = 0$, i.e., with zero intrinsic growth rates. If the interaction matrix A satisfies $a_{11} \neq a_{21}$ and $a_{22} \neq a_{12}$, by scaling (redefining) the components x_1, x_2 one can scale the columns of A so that

$$\mathsf{A} = \begin{pmatrix} -a_1 & 1 - a_2 \\ 1 - a_1 & -a_2 \end{pmatrix} \tag{2.1}$$

for some a_1, a_2. The resulting rather symmetric system

$$\begin{cases} \dot{x}_1 = x_1 \left[-a_1 \, x_1 + (1 - a_2) x_2 \right], \\ \dot{x}_2 = x_2 \left[+(1 - a_1) x_1 - a_2 \, x_2 \right] \end{cases} \tag{2.2}$$

has four invariant lines: the usual $x_1 = 0$, $x_2 = 0$ and the one at infinity, which plays no role here; also $x_1 - x_2 = 0$, since if $x_1 = x_2$ then $\dot{x}_1 = \dot{x}_2$. Only solutions $x = x(\tau)$ not lying along any of these lines will be considered. By examination,

$$I = |x_1|^{a_2} \, |x_2|^{a_1} \, |x_1 - x_2|^{1 - a_1 - a_2} \tag{2.3}$$

is a first integral: the reciprocal of the standard case-II first integral (1.3).

Define an auxiliary (new time) variable t by

$$t := (x_1 + x_2)/(x_2 - x_1), \tag{2.4}$$

so that $t = -1, 1, \infty$ correspond to the three just-mentioned invariant lines. The three t-intervals $(-\infty, -1)$, $(-1, 1)$, $(1, \infty)$ correspond to sectors in the x_1, x_2-plane lying between the lines. Thus in the first quadrant, the sectors $0 < x_2 < x_1$ and $0 < x_1 < x_2$ correspond to the t-intervals $(-\infty, -1)$ and $(1, \infty)$. To any solution $x = x(\tau)$ of the system (2.2) there is associated a function $t = t(\tau)$,

taking values in one of the three t-intervals. The value t_0 taken by t at the time-origin (say, at $\tau = 0$) determines the t-interval.

By calculus applied to (2.4) and the system (2.2), $t = t(\tau)$ satisfies

$$\frac{\ddot{t}}{\dot{t}^2} - \left(\frac{1-a_1}{t+1} + \frac{1-a_2}{t-1}\right) = 0, \tag{2.5}$$

which integrates to the hyperlogistic growth law

$$\dot{t} = A \times |t+1|^{1-a_1} |t-1|^{1-a_2}, \tag{2.6}$$

$A \neq 0$ being arbitrary. Hence viewed inversely as a function of t, τ is given by

$$\tau = A^{-1} \times \int_{t_0}^{t} |t'+1|^{a_1-1} |t'-1|^{a_2-1}\, dt'. \tag{2.7}$$

Moreover, it follows by differentiating (2.4) and exploiting (2.2) that

$$(x_1, x_2) = (x_1(t), x_2(t)) = \left(\frac{\dot{t}}{t+1}, \frac{\dot{t}}{t-1}\right). \tag{2.8}$$

Thus x_1, x_2 as well as τ can be expressed as functions of the new time t.

The integral in (2.7) defines an increasing function of t: an *incomplete beta function* $\tau = \mathrm{B}_{a_1,a_2;t_0}(t)$ with parameters a_1, a_2, as is explained in the appendix. It maps in an increasing way the t-interval containing t_0 onto some τ-interval, which may be infinite. The system (2.2) is thus solved parametrically by

$$\tau = \tau(t) = A^{-1} \times \mathrm{B}_{a_1,a_2;t_0}(t), \tag{2.9a}$$

$$(x_1, x_2) = (x_1(t), x_2(t)) = A \times |t+1|^{1-a_1} |t-1|^{1-a_2} \left(\frac{1}{t+1}, \frac{1}{t-1}\right), \tag{2.9b}$$

(2.9b) coming from (2.8). The parameter t is restricted to the relevant t-interval.

This is a *complete* integration of the $d = 2$ system (2.2), as the expressions for x_1, x_2 and τ as functions of the new time t involve two undetermined constants: A and t_0. (Other than determining the t-interval, the latter merely shifts τ.) Incomplete beta functions are supported by many software packages, so the numerical solution of any case-II $d = 2$ system is quite easy. Growth rates a_{10}, a_{20} that are nonzero but equal can readily be incorporated; see example 2.1 below.

One can also eliminate t, and at least formally express x_1, x_2 as functions of the original time τ. Let $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ be any convenient, standardized solution of the $A = 1$ case of the nonlinear ODE (2.6). (The function $\mathrm{B}^{-1}_{a_1,a_2}$ will map in an increasing way some τ-interval $(\tau_{\min}, \tau_{\max})$, which may be infinite, onto one of the t-intervals $(-\infty, -1)$, $(-1, 1)$, $(1, \infty)$; so it will depend on the choice of t-interval.) The general solution $x = x(\tau)$ of (2.2) is then given by (2.8) or (2.9b) with

$$t = \mathrm{B}^{-1}_{a_1,a_2}\big(A(\tau - \tau_0)\big), \tag{2.10}$$

which is defined if $A(\tau - \tau_0)$ lies in $(\tau_{\min}, \tau_{\max})$. The solution $x = x(\tau)$ thus contains two free parameters, A and τ_0, and implicitly a choice of t-interval, i.e. a choice of sector in the x_1, x_2-plane.

For this $x = x(\tau)$ to be more than formal, an explicit expression for the (standardized) inverse incomplete beta function $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ is needed. As the

appendix explains, expressions are available for some a_1, a_2. If the set $\{1/a_1, 1/a_2, 1/(1-a_1-a_2)\}$ is any of $\{1, m, -m\}$ (for m a positive integer), $\{1, \infty, \infty\}$, or $\{2, 2, \infty\}$, the inverse is expressible in terms of elementary functions; and if it is any of $\{2, 4, 4\}$, $\{2, 3, 6\}$, or $\{3, 3, 3\}$, in terms of elliptic ones. In each case the inverse extends to a one-valued function on the complex τ-plane. Thus $x = x(\tau)$ given by (2.9b) and (2.10), containing fractional powers, is at most finite-valued.

Table A.1 gives expressions for the (standardized) inverse function $t = \mathrm{B}_{a,a}^{-1}(\tau)$ when $a = 0, \frac{1}{4}, \frac{1}{3}, \frac{1}{2}, 1$. Each is one-valued on the τ-plane, as stated. It should also be noted that if a_1, a_2 are integers which are positive, or satisfy $a_1 a_2 < 0$ with $a_1 + a_2 \leqslant 0$, the inverse will be an *algebraic* function (and hence, finite-valued on the τ-plane). In these cases too, $x = x(\tau)$ will be finite-valued. In any of the preceding finite-valued cases, the Lotka–Volterra system (2.2) has by definition a weak form of the Painlevé property. This result seems to be new.

Example 2.1. Consider the symmetric system

$$\begin{cases} \dot{x}_1 = a_{*0}\, x_1 + x_1(-x_1 + 3\, x_2)/4, \\ \dot{x}_2 = a_{*0}\, x_2 + x_2(+3\, x_1 - x_2)/4, \end{cases} \tag{2.11}$$

where $x_1, x_2 > 0$ and $x_1 \neq x_2$ for simplicity. The state variables x_1, x_2 are the populations of species that grow logistically and also display mutualism: the growth of each is made more rapid by the presence of the other. Suppose initially that $a_{*0} = 0$, so that this is the case $a_1 = a_2 = 1/4$ of the system (2.2).

The auxiliary variable $t = (x_1 + x_2)/(x_2 - x_1)$ satisfies the interval condition $t \in (1, \infty)$ if (initially and hence subsequently) $0 < x_1 < x_2$; suppose this to be so. By table A.1 the standardized inverse function for this interval is

$$t = \mathrm{B}_{1/4,1/4}^{-1}(\tau) = \tfrac{1}{2}[\mathrm{cn}^2 + \mathrm{cn}^{-2}](\tau/2), \tag{2.12}$$

where cn is the Jacobian function with parameter $m = k^2 = 1/2$. The domain $(\tau_{\min}, \tau_{\max})$ is $(0, K_{1/4})$, where $K_{1/4} = \Gamma(\frac{1}{4})^2/2\Gamma(\frac{1}{2}) \approx 3.708$. Substituting (2.12) into (2.8) yields the general $0 < x_1 < x_2$ solution, parametrized by $A > 0$ and τ_0:

$$\big(x_1(\tau), x_2(\tau)\big) = A\left(\frac{\mathrm{sn}^3}{2\,\mathrm{cn}\,\mathrm{dn}}, \frac{2\,\mathrm{dn}^3}{\mathrm{sn}\,\mathrm{cn}}\right)\big(A(\tau - \tau_0)/2\big), \tag{2.13}$$

which is defined if $A(\tau - \tau_0)$ lies in $(0, K_{1/4})$. Here such elliptic-function identities as $\mathrm{sn}^2 + \mathrm{cn}^2 = 1$ and $m\,\mathrm{sn}^2 + \mathrm{dn}^2 = 1$ have been used. For this system the first integral (2.3) is $I = |x_1 x_2|^{1/4} |x_1 - x_2|^{1/2}$, and by examination $I \equiv \sqrt{2}\, A$.

The phase portrait in the $0 < x_1 < x_2$ sector is evident from (2.13). The endpoints $\tau_{\min} = 0$, $\tau_{\max} = K_{1/4}$, are zeroes of sn, cn respectively. So as $A(\tau - \tau_0) \to 0^+$, $t \to 1^+$ and (x_1, x_2) diverges to infinity while approaching the positive x_2-axis (an invariant line). Also as $A(\tau - \tau_0) \to K_{1/4}^-$, $t \to \infty$ and (x_1, x_2) diverges to infinity while approaching the $x_1 = x_2$ line (also invariant). These divergences are due to the strong mutualism. Although the solution (2.13) has a real τ-interval of width $A^{-1} K_{1/4}$ as its domain, it extends in a one-valued way to the complex τ-plane. Thus the system (2.11) has the Painlevé property.

Incorporating a nonzero common growth rate a_{*0} is straightforward, as noted in the introduction. Exponentially modifying the independent and dependent

variables yields the general $0 < x_1 < x_2$ solution, parametrized by real τ_1 and C:

$$\big(x_1(\tau), x_2(\tau)\big) = \mathrm{e}^{a_{*0}(\tau-\tau_1)} \left(\frac{\mathrm{sn}^3}{2\,\mathrm{cn}\,\mathrm{dn}}, \frac{2\,\mathrm{dn}^3}{\mathrm{sn}\,\mathrm{cn}} \right) \big((\mathrm{e}^{a_{*0}(\tau-\tau_1)} - C)/2\big), \tag{2.14}$$

which is defined if $\mathrm{e}^{a_{*0}(\tau-\tau_1)} - C$ lies in $(0, K_{1/4})$. Compared to the mutualism, the role played by any $a_{*0} > 0$ in causing finite-time blow-up is minor.

On the complex τ-plane the poles of any instance of the solution (2.13) lie on a square lattice, since $\mathrm{sn}, \mathrm{cn}, \mathrm{dn}$ are doubly periodic; but those of any instance of (2.14) lie on an exponentially stretched lattice. The pole locations are of interest because solutions in the complex time domain of non-integrable systems are expected to have irregular patterns of singularities (Bessis & Chafee 1986).

The just-concluded example was rather special, as setting $a_1 = a_2 = 1/4$ leads to one-valuedness on the complex τ-plane. It must be stressed that for generic a_1, a_2, owing to the presence of branch points the general complex-domain solution $(x_1(\tau), x_2(\tau))$ of the system (2.2) will not be one-valued or even finite-valued. The distribution of its poles over its many branches remains to be explored.

However, the example made clear the behaviour of any real-domain solution $(x_1(\tau), x_2(\tau))$ in the forward-time limit; i.e., as τ tends to the upper endpoint of its interval of definition. In the first quadrant, either the invariant line $x_1 = x_2$ will be an attractor (as in the example), or it will be a repeller and the lines $x_1 = 0$, $x_2 = 0$ will be attractors. In population ecology, if $a_1, a_2 > 1$ so that the two species compete rather than display mutualism, these two possibilities would be called competitive coexistence and exclusion (Maynard Smith 1974).

The analysis in this section of the case-II $d = 2$ system assumed for simplicity that $a_{11} \neq a_{21}$ and $a_{22} \neq a_{12}$. This can be relaxed. Suppose the growth rates are zero ($a_{10} = a_{20} = 0$) and say, that $a_{11} = a_{21} =: a_{*1}$. Then by examination the three usual invariant lines, namely $x_1 = 0$, $x_2 = 0$ and the one at infinity, have respective multiplicities $1, 2, 1$ in the sense of Christopher et al. (2007); and there are no others. (This configuration of lines is numbered 4.20 by Schlomiuk & Vulpe (2010).) The line $x_2 = 0$ thus has an extra (generalized) Darboux polynomial associated to it. The first integral (1.3) is accordingly replaced by

$$I = |x_1|^{a_{22}}\, |x_2|^{-a_{12}} \exp(a_{*1} x_1/x_2), \tag{2.15}$$

exhibiting the DP's x_1, x_2 and the extra generalized DP. It is convenient to choose as the new time variable $s := x_1/x_2$. The ODE (2.5) is then replaced by

$$\frac{\ddot{s}}{\dot{s}^2} = \frac{1}{a_{12} - a_{22}} \left(\frac{a_{12}}{s} + a_{*1} \right). \tag{2.16}$$

This can be integrated to express $\tau = \tau(s)$ in terms of an incomplete gamma function, or alternatively (if $a_{22} = -a_{12}$) the error function erf. This sheds light on the solution of a particular Lotka–Volterra system with $a_{11} = a_{21}$, involving erf and erf^{-1}, that was recently published (Chandrasekar et al. 2007, § 4.2).

3. Three-dimensional integration

(a) *General case-II$_i$ systems*

It will now be shown that an unexpectedly large family of $d=3$ Lotka–Volterra systems of the form (1.1) can be integrated parametrically by the technique of § 2. These are case-II$_i$ systems as defined in table 2; specifically, systems with $a_{ji} = a_{ki} =: a_{*i}$, so that the species j,k other than i have equal effects on species i. Without loss of generality $i=3$ and $(j,k)=(1,2)$ will be taken. Initially it will be assumed that $a_{10}=a_{20}=a_{30}=0$, i.e., that the intrinsic growth rates are zero, though including rates that are nonzero but equal is an easy matter.

Systems in this family include certain ABC and symmetric May–Leonard models, which are treated as examples in §§ 3b and 3c. Besides constructing explicit solutions, one can determine from powerful results of Carton-LeBrun (1969) precisely which systems in the family have the Painlevé property that each solution $x=x(\tau)$ extends in a one-valued way to the complex τ-plane. Generalized case-II$_i$ systems which have unequal growth rates will be examined in § 4.

Suppose $a_{13}=a_{23}=:a_{*3}$. If the interaction matrix A satisfies $a_{11}\neq a_{21}$, $a_{22}\neq a_{12}$ and $a_{33}\neq a_{*3}\neq 0$, by scaling (redefining) the components x_1,x_2,x_3 one can scale the columns of A so that

$$\mathsf{A} = \left(\begin{array}{cc|c} -a_1 & 1-a_2 & 1 \\ 1-a_1 & -a_2 & 1 \\ \hline b_1-a_1 & b_2-a_2 & -1/n \end{array}\right) \tag{3.1}$$

for some $a_1,a_2;b_1,b_2$ and $n\neq 0,-1$. ($n=\infty$ will signify $1/n=0$.) The system

$$\begin{cases} \dot{x}_1 = x_1\left[-a_1x_1+(1-a_2)x_2+x_3\right], \\ \dot{x}_2 = x_2\left[+(1-a_1)x_1-a_2x_2+x_3\right], \\ \dot{x}_3 = x_3\left[(b_1-a_1)x_1+(b_2-a_2)x_2-x_3/n\right], \end{cases} \tag{3.2}$$

which reduces to the $d=2$ system (2.2) when $x_3\equiv 0$, has five invariant planes: the usual $x_1=0$, $x_2=0$, $x_3=0$ and the one at infinity, which plays no role here; also $x_1-x_2=0$, since if $x_1=x_2$ then $\dot{x}_1=\dot{x}_2$. Solutions $x=x(\tau)$ not lying in any of these planes are of primary interest. By examination,

$$I = |x_1|^{\bar{n}a_2-b_2}\,|x_2|^{\bar{n}a_1-b_1}\,|x_3|\;|x_1-x_2|^{\bar{n}(1-a_1-a_2)-(1-b_1-b_2)} \tag{3.3}$$

is the specialization of the case-II$_3$ first integral (1.4). Here and below,

$$\bar{n} := (n+1)/n \tag{3.4}$$

for convenience; note that $\bar{n}\neq 0$, with $\bar{n}=1$ meaning $n=\infty$, i.e., $1/n=0$.

Define an auxiliary variable t as in § 2 by

$$t := (x_1+x_2)/(x_2-x_1), \tag{3.5}$$

so that $t=-1,1,\infty$ correspond to the planes $x_1=0$, $x_2=0$ and $x_1-x_2=0$. Thus $0<x_2<x_1$ and $0<x_1<x_2$ correspond to the t-intervals $(-\infty,-1)$ and $(1,\infty)$. The function $t=t(\tau)$ associated to any trajectory $x=x(\tau)$ takes values in one of the intervals $(-\infty,-1)$, $(-1,1)$, $(1,\infty)$. On any portion of $x=x(\tau)$ on which $\dot{t}$ does not change sign, t can be used as an alternative parameter: a new time.

By repeatedly differentiating (3.5) to obtain formulas for $t, \dot{t}, \ddot{t}$ and $\dddot{t}$, each time exploiting (3.2), and eliminating x_1, x_2, x_3 from these formulas, one finds

$$
\begin{aligned}
&\frac{\dddot{t}}{\dot{t}^3} + (\bar{n}-2)\left(\frac{\ddot{t}}{\dot{t}^2}\right)^2 + \left[\frac{1-b_1-2\bar{n}(1-a_1)}{t+1} + \frac{1-b_2-2\bar{n}(1-a_2)}{t-1}\right]\frac{\ddot{t}}{\dot{t}^2} \\
&\quad + \left\{\frac{(1-a_1)\left[b_1+\bar{n}(1-a_1)\right]}{(t+1)^2} + \frac{(1-a_2)\left[b_2+\bar{n}(1-a_2)\right]}{(t-1)^2}\right. \qquad (3.6) \\
&\qquad \left. - \frac{(1-a_1)[b_1+\bar{n}(1-a_1)]+(1-a_2)[b_2+\bar{n}(1-a_2)]+(2-a_1-a_2)[(1-b_1-b_2)-\bar{n}(2-a_1-a_2)]}{(t+1)(t-1)}\right\} = 0,
\end{aligned}
$$

which is the $d=3$ counterpart of (2.5). The nonlinear third-order ODE (3.6) will be called a *generalized Schwarzian equation* (gSE), since when $\bar{n}=1/2$ (i.e., $n=-2$) its first two terms constitute a Schwarzian derivative, and if additionally $b_1=a_1$, $b_2=a_2$ so that its two $\ddot{t}/\dot{t}^2$ terms vanish, it becomes a Schwarzian equation of a type familiar from the conformal mapping of triangles (Nehari 1952).

The seemingly complicated gSE (3.6), with solution $t=t(\tau)$, can be integrated without difficulty. Suppose for simplicity that $\dot{t}>0$. Let $\dot{t} =: f^{-1/\bar{n}}$, i.e., $f := \dot{t}^{\bar{n}}$, and view t, f (rather than τ, t) as the independent and dependent variables. By applying the chain rule $\mathrm{d}/\mathrm{d}\tau = \dot{t}\, D_t = f^{1/\bar{n}} D_t$ where $D_t := \mathrm{d}/\mathrm{d}t$, one finds that

$$
\begin{aligned}
&\left\{D_t^2 + \left[\frac{1-b_1-2\bar{n}(1-a_1)}{t+1} + \frac{1-b_2-2\bar{n}(1-a_2)}{t-1}\right]D_t\right. \\
&\quad + \bar{n}\left\{\frac{(1-a_1)\left[b_1+\bar{n}(1-a_1)\right]}{(t+1)^2} + \frac{(1-a_2)\left[b_2+\bar{n}(1-a_2)\right]}{(t-1)^2}\right. \qquad (3.7) \\
&\qquad \left.\left. - \frac{(1-a_1)[b_1+\bar{n}(1-a_1)]+(1-a_2)[b_2+\bar{n}(1-a_2)]+(2-a_1-a_2)[(1-b_1-b_2)-\bar{n}(2-a_1-a_2)]}{(t+1)(t-1)}\right\}\right\} f = 0
\end{aligned}
$$

is the ODE (surprisingly, a linear one) satisfied by $f=f(t)$. This ODE is a so-called Papperitz equation, which can be greatly simplified by a substitution of a standard type. Substituting $f=(t+1)^{\bar{n}(1-a_1)}(t-1)^{\bar{n}(1-a_2)}\,g$ reduces it to the degenerate hypergeometric equation

$$
\left\{D_t^2 + \left[\frac{1-b_1}{t+1} + \frac{1-b_2}{t-1}\right]D_t\right\} g = 0, \tag{3.8}
$$

which can be integrated by inspection. In this way one deduces that

$$
\begin{aligned}
\dot{t}^{\bar{n}} = f(t) &= |t+1|^{\bar{n}(1-a_1)}\,|t-1|^{\bar{n}(1-a_2)}\left[K_1 + K_2\int_{t_0}^{t} |t'+1|^{b_1-1}|t'-1|^{b_2-1}\,dt'\right] \\
&= |t+1|^{\bar{n}(1-a_1)}\,|t-1|^{\bar{n}(1-a_2)}\left[K_1 + K_2\,\mathrm{B}_{b_1,b_2;t_0}(t)\right],
\end{aligned} \tag{3.9}
$$

where K_1, K_2 are undetermined constants and t_0 is any convenient point in the relevant t-interval. For the incomplete beta function $\mathrm{B}_{b_1,b_2;t_0}(t)$, see the appendix.

Formulas for the inverse function $\tau=\tau(t)$ and the alternatively parametrized trajectory $x=x(t)$ of the system (3.2) follow immediately from (3.9). The

restriction $\dot{t} > 0$ will now be dropped: suppose instead that on the portion of the trajectory under study, $\pm\dot{t} > 0$. By integrating $\mathrm{d}\tau/\mathrm{d}t = \dot{t}^{-1}$ one obtains

$$\tau = \tau(t) = \tau_0 \pm \int_{t_0}^{t} |t'+1|^{a_1-1}|t'-1|^{a_2-1} \left|K_1 + K_2\,\mathrm{B}_{b_1,b_2;t_0}(t')\right|^{1/(n+1)-1}\,dt', \tag{3.10a}$$

$$(x_1,x_2,x_3) = (x_1(t),x_2(t),x_3(t)) = \left(\frac{\dot{t}}{t+1}, \frac{\dot{t}}{t-1}, \frac{\ddot{t}}{\dot{t}} - (1-a_1)\frac{\dot{t}}{t+1} - (1-a_2)\frac{\dot{t}}{t-1}\right). \tag{3.10b}$$

In (3.10a), t is restricted to the relevant t-interval (containing any conveniently chosen point t_0) and is further restricted by the requirement that the quantity $K_1 + K_2\,\mathrm{B}_{b_1,b_2;t_0}(t')$, within absolute value signs, not change sign. The accompanying formulas (3.10b), which extend the $d=2$ formula (2.8), are an easy exercise. They come by reverting the abovementioned expressions for $t, \dot{t}, \ddot{t}$ as rational functions of x_1,x_2,x_3. In practice one would compute $\dot{t}, \ddot{t}$ in (3.10b) by applying $\dot{t} = (\mathrm{d}\tau/\mathrm{d}t)^{-1}$ and $\ddot{t} = \dot{t}(\mathrm{d}/\mathrm{d}t)\dot{t}$ to (3.10a).

The parametric solution $(\tau, x) = (\tau(t), x(t))$ displayed in (3.10) is the central result of this paper. It is a *complete* integration of the $d=3$ Lotka–Volterra system (3.2), as the expressions for τ and x_1,x_2,x_3 as functions of t involve three undetermined constants: the coefficients K_1, K_2, and also τ_0 (which merely shifts τ). Growth rates a_{10}, a_{20}, a_{30} that are nonzero but equal can easily be incorporated in (3.10), as when $d=2$. The solution (3.10) subsumes the $d=2$ solution (2.9). This is because if $K_2 = 0$ then $\tau = \tau(t)$ given by (3.10a) reduces to (2.9a), and $x_3 = x_3(\tau)$ computed from (3.10b) will be identically zero.

Example 3.1. Consider a $d=3$ Lotka–Volterra system of the form (3.2) with $b_1 = a_1$, $b_2 = a_2$, so that species 3 is unaffected by species 1 and 2. In this case $(\tau,x) = (\tau(t), x(t))$ can be simplified, since if $K_2 \neq 0$, Eq. (3.10a) integrates to

$$\tau = \tau(t) = \tau_0 \pm \begin{cases} |K_2|^{-1}\left\{|K_1 + K_2\,\mathrm{B}_{a_1,a_2;t_0}(t)|^{1/(n+1)} - |K_1|^{1/(n+1)}\right\} & n \text{ finite}, \\ |K_2|^{-1}\ln|1 + (K_2/K_1)\mathrm{B}_{a_1,a_2;t_0}(t)| & n = \infty. \end{cases} \tag{3.11}$$

In terms of a standardized inverse beta function $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ as discussed in the appendix (and used in § 2), this simply says that $t = t(\tau)$ is of the form

$$t = t(\tau) = \begin{cases} \mathrm{B}^{-1}_{a_1,a_2}\left((A\tau+B)^{n+1} + C\right), & n \text{ finite}, \\ \mathrm{B}^{-1}_{a_1,a_2}\left(\exp(A\tau+B) + C\right), & n = \infty, \end{cases} \tag{3.12}$$

for some $A \neq 0, B, C$. For a_1, a_2 for which $\mathrm{B}^{-1}_{a_1,a_2}(\tau)$ is expressible in terms of standard functions, such as in those in table A.1, this allows $x = x(\tau)$ when $b_1 = a_1$, $b_2 = a_2$ to be similarly expressed, by substituting (3.12) into (3.10b).

For many a_1, a_2, such as those in the table, the function $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ has a one-valued extension to the complex τ-plane. For such a_1, a_2, if n is an *integer* ($n \neq 0, -1$) or $n = \infty$, the system (3.2) with $b_1 = a_1$, $b_2 = a_2$ will have the Painlevé property. This is because if n is an integer or ∞, $t = t(\tau)$ in (3.12) and likewise $x = x(\tau)$ will extend to the τ-plane with no branchpoint at $\tau = -B/A$, i.e., in a one-valued way. But in each such system, the third species decouples.

One can also determine which $d = 3$ Lotka–Volterra systems of the form (3.2), *with no species decoupled*, have the Painlevé property; and in fact, integrate each such explicitly. In the gSE (3.6) for $t = t(\tau)$ there are seven terms and thus seven coefficients, the first two being 1 and $\bar{n} - 2 = 1/n - 1$. Suppose the remaining five are not determined by $a_1, a_2; b_1, b_2$ and n, as here, but are free to vary. For some choices of these five the resulting nonlinear ODE will have the Painlevé property. By a mathematically rigorous analysis Carton-LeBrun (1969) determined, classified and tabulated the many possibilities, and integrated each resulting ODE. Hence all one needs to do is compare the coefficients in the gSE (3.6) against her tables to determine for which $a_1, a_2; b_1, b_2$ and n all solutions $t = t(\tau)$ of the gSE will extend in a one-valued way to the τ-plane. For each such choice one can compute $x = x(\tau)$ from (3.10b), and it will extend similarly; thus the case-II$_3$ system (3.2) as well as the gSE will have the Painlevé property.

It is not hard to see that for the gSE (3.6) to have the Painlevé property the parameter n must be an integer ($n \neq 0, -1$ as usual) or ∞; else the gSE would have complex-domain solutions $t = t(\tau)$ with movable branchpoints. The tables of Carton-LeBrun include infinite families of gSE's in which n is otherwise unconstrained, such as ones with $b_1 = a_1$, $b_2 = a_2$ that were implicitly encountered in example 3.1. They also include many gSE's with $n = 1, 2, 3, 5$ or ∞. Each can be twice integrated to yield a polynomial identity $P(t, \dot{t}; K_1, K_2) = 0$ with parameters K_1, K_2, the identities appearing in her table VIII. Any solution $t = t(\tau)$ is thus reduced to quadratures. For nearly all of these gSE's, solutions $t = t(\tau)$ and hence trajectories $x = x(\tau)$ can be expressed in terms of elliptic functions (lemniscatic or equianharmonic); for a few, in terms of elementary functions.

Example 3.2. Consider the $d = 3$ Lotka–Volterra system

$$\begin{cases} \dot{x}_1 = a_{*0}\, x_1 + x_1(x_2 + x_3), \\ \dot{x}_2 = a_{*0}\, x_2 + x_2(x_1 + x_3), \\ \dot{x}_3 = a_{*0}\, x_3 + x_3(x_1 - 2\,x_2 - x_3), \end{cases} \tag{3.13}$$

where for simplicity $x_1, x_2, x_3 > 0$ and $x_1 \neq x_2$. The state variables x_1, x_2, x_3 are the populations of three species with common intrinsic growth rate a_{*0}. If $a_{*0} > 0$ then in isolation species 3, though not 1 or 2, grows logistically. Species 1 and 2 display mutualism, as do 1 and 3; and species 2 preys on species 3.

Since a nonzero a_{*0} is easy to incorporate, set $a_{*0} = 0$. System (3.13) is then the case $(a_1, a_2; b_1, b_2; n) = (0, 0; 1, -2; 1)$ of (3.2). With these values the gSE (3.6) for $t = t(\tau)$ is a variant of Carton-LeBrun's $n = 1$ case II. Integrating twice yields

$$\dot{t}^2 = K_1(t^2 - 1)^2 + K_2(t + 1)^2, \tag{3.14}$$

where K_1, K_2 are undetermined constants. (As $\dot{t}^{\bar{n}} = \dot{t}^2 = f(t)$, the right side is the general solution of the Papperitz equation (3.7).) Integrating once more yields

$$t = (x_1 + x_2)/(x_2 - x_1) = \frac{3 + (c_1 - c_2\,\cos\tau)}{1 - (c_1 - c_2\,\cos\tau)} \tag{3.15}$$

as the general solution of the gSE. Here c_1, c_2 are constrained by $c_1^2 - c_2^2 = 1$ and τ can be replaced by $A\tau + B$, for any $A \neq 0$ and B.

Substituting (3.15) into (3.10b) yields

$$(x_1, x_2, x_3)(\tau) = \left(\frac{c_2 \sin\tau}{1-(c_1-c_2\cos\tau)}, \frac{2\,c_2 \sin\tau}{1-(c_1-c_2\cos\tau)^2}, \frac{-c_2+(1+c_1)\cos\tau}{[1+(c_1-c_2\cos\tau)]\sin\tau}\right) \tag{3.16}$$

as the general solution $x = x(\tau)$ of the system (3.13) with $a_{*0} = 0$, it being understood that τ can be replaced by $A\tau + B$, with x scaled by A. There are three degrees of freedom: A, B and the point on the hyperbola $c_1^2 - c_2^2 = 1$.

The first integral I of (3.3) specializes to $x_1^2|x_2^{-1}x_3|$, and by examination $I \equiv A^2 \times |c_1+1|/2$. The existence of a explicit general solution facilitates the study of global dynamics.

Example 3.3. Consider the $d = 3$ Lotka–Volterra system

$$\begin{cases} \dot{x}_1 = x_1\left[-\frac{1}{r}\,x_1 + (1+\frac{1}{r})x_2 + x_3\right], \\ \dot{x}_2 = x_2\left[+(1-\frac{1}{r})x_1 + \frac{1}{r}\,x_2 + x_3\right], \\ \dot{x}_3 = x_3\left[\frac{3}{r}\,x_1 - \frac{3}{r}\,x_2 - x_3\right], \end{cases} \tag{3.17}$$

where $r \neq 0$, and for simplicity $x_1, x_2, x_3 > 0$ and $x_1 \neq x_2$. The system (3.13) is the case $(a_1, a_2; b_1, b_2; n) = (\frac{1}{r}, -\frac{1}{r}; \frac{4}{r}, -\frac{4}{r}; 1)$ of (3.2). With these values the gSE (3.6) for $t = t(\tau)$ is a variant of Carton-LeBrun's case e.IV. The gSE can be integrated twice to yield $t = (u^r+1)/(u^r-1)$, where u is a solution of

$$\dot{u}^2 = K_1 u^4 - K_2 \tag{3.18}$$

and K_1, K_2 are undetermined constants. (To confirm this, it is easiest not to integrate the gSE itself, but rather the Papperitz equation (3.7) or preferably the degenerate hypergeometric equation (3.8), which are equivalent.) By integrating (3.18) once more, one deduces that $u \propto \mathrm{cn}(\tau)$ and thus that

$$t = (x_1+x_2)/(x_2-x_1) = \frac{C\,\mathrm{cn}^r+1}{C\,\mathrm{cn}^r-1}(\tau). \tag{3.19}$$

Here cn is the 'lemniscatic' Jacobian elliptic function with modular parameter $m = k^2 = 1/2$, and C is arbitrary; and as above, τ can be replaced by $A\tau + B$.

Substituting the expression (3.19) into (3.10b) yields

$$(x_1, x_2, x_3)(\tau) = \left(\frac{r\,\mathrm{sn}\,\mathrm{dn}}{(C\,\mathrm{cn}^r-1)\mathrm{cn}}, \frac{C\,r\,\mathrm{sn}\,\mathrm{dn}\,\mathrm{cn}^{r-1}}{C\,\mathrm{cn}^r-1}, \frac{\mathrm{cn}^3}{\mathrm{sn}\,\mathrm{dn}}\right)(\tau) \tag{3.20}$$

as the general solution $x = x(\tau)$ of the system (3.17), it being understood that τ can be replaced by $A\tau + B$, with x scaled by A. The first integral I of (3.3) specializes to $|x_1/x_2|^{2/r}|x_3(x_1-x_2)|$, and by examination $I \equiv A^2 \times |r||C|^{-2/r}$. If r is an integer then (3.20) like (3.16) will be one-valued on the complex τ-plane; thus the system (3.17) like (3.13) will have the Painlevé property.

(*b*) *ABC systems*

An interesting application of the results of the last subsection is to a well-known family of ABC systems, which as explained in § 1 *b* are (generic) $d=3$ Lotka–Volterra systems without self-interactions. Any ABC system, with interaction matrix $\mathsf{A}=(a_{ij})_{i,j=1}^{3}$ given by (1.7), is of the form

$$\begin{cases} \dot y_1 = y_1(A_2\, y_2 + y_3), \\ \dot y_2 = y_2(A_3\, y_3 + y_1), \\ \dot y_3 = y_3(A_1\, y_1 + y_2). \end{cases} \tag{3.21}$$

It is known that when one of A_1, A_2, A_3 equals unity the ABC system is completely integrable in that a pair of first integrals exists, one of them being of the Darboux polynomial type (Grammaticos et al. 1990). But no general solution of ABC systems of this type has previously been published. From our point of view the integrability comes from an ABC system with $A_i=1$ being a case-II$_i$ system as defined in table 2. This facilitates a complete integration.

Suppose without loss of generality that $A_3=1$, and also that $A_2\neq 0$. In terms of a scaled state vector $(x_1,x_2,x_3):=(y_1,A_2y_2,y_3)$ the system becomes

$$\begin{cases} \dot x_1 = x_1(x_2 + x_3), \\ \dot x_2 = x_2(x_1 + x_3), \\ \dot x_3 = x_3(A_1\, x_1 + A_2^{-1}x_2), \end{cases} \tag{3.22}$$

which is the $(a_1,a_2;b_1,b_2;n)=(0,0;A_1,A_2^{-1};\infty)$ case of the case-II$_3$ system (3.2). An integration of (3.22) therefore follows at once from the complete integration (3.10). (As above, solutions that do not lie in any of the invariant planes $x_1=0$, $x_2=0$, $x_1-x_2=0$ are of primary interest.)

The new time $t:=(x_1+x_2)/(x_2-x_1)$ is used as the parameter. Along any segment of a trajectory $x=x(\tau)$ on which $\pm(\dot t = \mathrm{d}t/\mathrm{d}\tau)>0$, the variables τ and $x=(x_1,x_2,x_3)$ are expressed as functions of t by

$$\tau(t)=\tau_0 \pm \int_{t_0}^{t} \Big|\, \big[(t')^2-1\big]\,\big[K_1+K_2\,\mathrm{B}_{A_1,A_2^{-1};\,t_0}(t')\big]\,\Big|^{-1}\,dt', \tag{3.23a}$$

$$(x_1(t),x_2(t),x_3(t))=\left(\frac{\dot t}{t+1},\ \frac{\dot t}{t-1},\ \frac{\ddot t}{\dot t}-\frac{\dot t}{t+1}-\frac{\dot t}{t-1}\right). \tag{3.23b}$$

Here τ_0 is the initial time, at which $t=t_0$. The parameter t is restricted to whichever of $(-\infty,-1)$, $(-1,1)$, $(1,\infty)$ contains t_0. It may be further restricted by the additional condition that $K_1+K_2\,\mathrm{B}_{A_1,A_2^{-1};\,t_0}(t')$, within the absolute value signs, not change sign over the integration interval. The derivatives $\dot t, \ddot t$ in (3.23b) are computed by applying $\dot t = (\mathrm{d}\tau/\mathrm{d}t)^{-1}$ and $\ddot t = \dot t(\mathrm{d}/\mathrm{d}t)\dot t$ to (3.23a).

The parametric general solution (3.23) is a complete integration of the ABC system with $A_3=1$, since the expressions for τ and x_1,x_2,x_3 involve three undetermined constants: K_1,K_2 and also τ_0 (which merely shifts τ). For many choices of A_1,A_2 the expressions for τ and x_1,x_2,x_3 in terms of t can be expressed using elementary functions. This is because for many choices of b_1,b_2 the

incomplete beta function $\mathrm{B}_{b_1,b_2;t_0}(t)$ in (3.23a) can be so expressed. The evaluation of τ and x_1, x_2, x_3 is especially easy if $\mathrm{B}_{b_1,b_2;t_0}(t)$ is a rational function of t.

Example 3.4. Consider the case $(A_1, A_2, A_3) = (1, 1, 1)$ of the ABC system (3.21) and hence of (3.22), for which $(a_1, a_2; b_1, b_2; n) = (0, 0; 1, 1; \infty)$. When $t > 1$, as is the case for any trajectory $x = x(\tau)$ in the sector $0 < x_1 < x_2$, the definition (A.2) implies that $\mathrm{B}_{1,1;t_0}(t)$ equals t plus a constant. Substituting into (3.23) and evaluating the integral and derivatives yields

$$\tau(t) = \frac{\ln(t+C)}{C^2-1} + \frac{\ln(t+1)}{2(1-C)} + \frac{\ln(t-1)}{2(1+C)}, \tag{3.24a}$$

$$(x_1, x_2, x_3)(t) = \left((t-1)(t+C),\ (t+1)(t+C),\ t^2-1\right), \tag{3.24b}$$

where C is a constant; and one can also replace τ by $A\tau + B$ and scale (x_1, x_2, x_3) by A. Thus there are three undetermined constants in all.

The solution $x = x(\tau)$ in the sector is generated parametrically by allowing t to range over $(1, \infty)$, or perhaps (depending on C) a proper sub-interval. (The latter is because $t > 1$ covers $0 > x_1 > x_2$ as well as $0 < x_1 < x_2$.) The first integral I of (3.3) specializes to $|x_1^{-1} x_2^{-1} x_3 (x_1 - x_2)^2|$, and by examination $I \equiv 4|A|$.

Trajectories in other sectors, such as $0 < x_2 < x_1$, are generated similarly. The general solution (3.24) resembles but is more explicit than a solution of the ABC system with $(A_1, A_2, A_3) = (1, 1, 1)$ obtained by Abenda et al. (2001, § 7).

For any ABC system of the form (3.22), the new time $t = t(\tau)$ satisfies the generalized Schwarzian equation (3.6) with $(a_1, a_2; b_1, b_2; n) = (0, 0; A_1, A_2^{-1}; \infty)$. (That $n = \infty$ implies $\bar{n} = 1$.) Several of the gSE's listed by Carton-LeBrun (1969) as having the Painlevé property, in that all solutions $t = t(\tau)$ extend to a one-valued way to the complex plane, have $n = \infty$ and $a_1 = a_2 = 0$. They therefore give rise to ABC systems with $A_3 = 1$ that have the Painlevé property.

Example 3.5. Consider the case $(A_1, A_2, A_3) = (-1/2, -2, 1)$ of the ABC system (3.21) and hence of (3.22), for which $(a_1, a_2; b_1, b_2; n) = (0, 0; -1/2, -1/2; \infty)$. With these values the gSE (3.6) satisfied by $t = t(\tau)$ is a variant of Carton-LeBrun's case e.IV.3. The solution of this gSE is

$$t(\tau) = \left[(C \tanh \tau) + (C \tanh \tau)^{-1}\right] / 2, \tag{3.25}$$

where $C \neq 0$ is arbitrary and τ can be replaced by $A\tau + B$. (This is best shown by integrating the hypergeometric equation (3.8), though one could also integrate Eq. (3.23a), as in the last example.) Substituting (3.25) into (3.23b) gives

$$(x_1, x_2, x_3)(\tau) = \tag{3.26}$$

$$\left(\frac{-\cosh + C \sinh}{\sinh \cosh\,(\cosh + C \sinh)}, \frac{-\cosh - C \sinh}{\sinh \cosh\,(\cosh - C \sinh)}, \frac{2(1-C^2)\sinh \cosh}{C^2 \sinh^2 - \cosh^2} \right)(\tau),$$

where again τ can be replaced by $A\tau + B$, in which case (x_1, x_2, x_3) is scaled by A. Thus there are three undetermined constants in all.

Equation (3.26) provides a complete integration of the ABC system with $(A_1, A_2, A_3) = (-1/2, -2, 1)$. If $-1 < C < 1$ the trajectory defined by (3.26) with $\tau < 0$ lies in the positive orthant; and if $C = 0$ it lies in the plane $x_1 - x_2 = 0$.

If $C = \pm 1$ it lies in the plane $x_3 = 0$. The first integral I of (3.3) specializes to $|x_1 x_2|^{1/2} |x_3/(x_1 - x_2)|$, and by examination $I \equiv |A| \times |(C^2 - 1)/2C|$.

This system is of much interest, as it is the $A_3 = 1$ member of a family of ABC systems (with $A_1 = -1/(A_3 + 1)$ and $A_2 = -(A_3 + 1)/A_3$ for $A_3 \neq 0, -1$), each of which has the Painlevé property and is completely integrable (Bountis et al. 1984). Each has a first integral that is quadratic in x_1, x_2, x_3 (Strelcyn & Wojciechowski 1988). If $A_3 = 1$ this extra first integral is $J = (x_1 - x_2)^2 + 4x_3(x_1 + x_2 + x_3)$, and by examination $J \equiv A^2 \times 16$, irrespective of the integration constant C.

Bountis et al. remark that the member with $(A_1, A_2, A_3) = (-1/2, -2, 1)$ can be integrated with the aid of elliptic functions; but as Eq. (3.26) reveals, sinh and cosh suffice. This explicit general solution also makes manifest the one-valuedness of the continuation of $x = x(\tau)$ to the complex τ-plane.

(*c*) *Symmetric May–Leonard systems*

A particularly striking application of the results of § 3 *a* is to the integration of certain May–Leonard systems. As was explained in § 1 *b*, the three species in any May–Leonard system compete cyclically, with α, β being the strength of clockwise and counter-clockwise interactions. The systems of interest here are those with $\alpha = \beta$, for which the species are equivalent; they are completely integrable. An explicit general solution will be obtained for the first time: see Eqs. (3.29)–(3.30) below. The system with $\alpha = \beta = -1$, which is mutualistic rather than competitive, will be shown to have the Painlevé property. May–Leonard systems have been analysed from the Painlevé point of view (Bountis & Segur 1982; Sachdev & Ramanan 1997) and multiple first integrals have been discovered (Llibre & Valls 2011; Tudoran & Gîrban 2012). But the results below are much more explicit.

Suppose that $a_{10} = a_{20} = a_{30} = 0$, i.e., that the intrinsic growth rates are zero, since including rates that are nonzero but equal is easy. The system (1.1), with the May–Leonard interaction matrix (1.8) and $\alpha = \beta$, is then of the form

$$\begin{cases} \dot{y}_1 = y_1(-y_1 - \alpha\, y_2 - \alpha\, y_3), \\ \dot{y}_2 = y_2(-\alpha\, y_1 - y_2 - \alpha\, y_3), \\ \dot{y}_3 = y_3(-\alpha\, y_1 - \alpha\, y_2 - y_3). \end{cases} \tag{3.27}$$

Suppose that $\alpha \neq 0, 1$. Then in terms of a scaled state vector $(x_1, x_2, x_3) := ((1-\alpha)y_1,\ (1-\alpha)y_2,\ -\alpha y_3)$, the system becomes

$$\begin{cases} \dot{x}_1 = x_1(-\tfrac{1}{1-\alpha}\, x_1 - \tfrac{\alpha}{1-\alpha}\, x_2 + x_3), \\ \dot{x}_2 = x_2(-\tfrac{\alpha}{1-\alpha}\, x_1 - \tfrac{1}{1-\alpha}\, x_2 + x_3), \\ \dot{x}_3 = x_3(-\tfrac{\alpha}{1-\alpha}\, x_1 - \tfrac{\alpha}{1-\alpha}\, x_2 + \tfrac{1}{\alpha}\, x_3), \end{cases} \tag{3.28}$$

which is the $(a_1, a_2; b_1, b_2; n) = \big((1-\alpha)^{-1},\ (1-\alpha)^{-1};\ 1, 1;\ -\alpha\big)$ case of the case-II$_3$ system (3.2). An integration scheme therefore follows at once from the complete integration (3.10). As above, it will yield all solutions that do *not* lie in any of the invariant planes $x_1 = 0$, $x_2 = 0$, $x_1 - x_2 = 0$.

The new time variable $t := (x_1 + x_2)/(x_2 - x_1)$ plays its familiar role. Along any segment of a trajectory $x = x(\tau)$ on which $\pm(\dot{t} = \mathrm{d}t/\mathrm{d}\tau) > 0$, the function $t = t(\tau)$ satisfies

$$\dot{t} = \pm \left|(t^2 - 1)(K_1\, t + K_2)\right|^{\alpha/(\alpha-1)} \tag{3.29}$$

where K_1, K_2 are constants. This is a specialization of (3.10a), since according to the definition (A.2), $\mathrm{B}_{1,1;t_0}(t)$ equals t plus a constant. After obtaining $t = t(\tau)$ by integrating Eq. (3.29), one would substitute it into (3.10b), i.e., into

$$(x_1(\tau), x_2(\tau), x_3(\tau)) = \left(\frac{\dot{t}}{t+1}, \frac{\dot{t}}{t-1}, \frac{\ddot{t}}{\dot{t}} + \frac{\alpha}{1-\alpha}\left(\frac{\dot{t}}{t+1} + \frac{\dot{t}}{t-1}\right)\right), \tag{3.30}$$

to obtain the components of $x = x(\tau)$. This scheme is readily carried out, either numerically or (for certain α) symbolically. Thus one can, *inter alia*, confirm the results of Blé et al. (2013) on the global dynamics of $\alpha = \beta$ May–Leonard systems.

Example 3.6. Suppose $\alpha = m/(m+1)$, for m a positive integer. Then the exponent $\alpha/(\alpha-1)$ in (3.29) equals $-m$, and $\mathrm{d}\tau/\mathrm{d}t = \dot{t}^{-1}$ is a degree-$3m$ polynomial in t. Hence τ is a degree-$(3m+1)$ polynomial, and its inverse $t = t(\tau)$ is algebraic. By substituting this function into (3.30) one deduces that on the complex τ-plane, each of x_1, x_2, x_3 is also an algebraic (finite-branched) function.

Hence when $\alpha = \beta = m/(m+1)$, the May–Leonard system has a weak form of the Painlevé property. This result appears to be new. The simplest case is when $\alpha = 1/2$ (corresponding to $m = 1$), when τ is quartic in t. By applying the quartic formula one can express $t = t(\tau)$ and hence each $x_i = x_i(\tau)$ in terms of radicals.

Example 3.7. Let $\alpha = \beta = -1$, so that $(a_1, a_2; b_1, b_2; n) = (1/2, 1/2; 1, 1; 1)$. When $\alpha = -1$ the solution of the ODE (3.29) can be expressed using the Weierstrassian elliptic function $\wp(\tau) = \wp(\tau; g_2, g_3)$, with $\dot{\wp}^2 = 4\wp^3 - g_2\wp - g_3$. One notes that the gSE (3.6), also satisfied by $t = t(\tau)$, is an ODE listed by Carton-LeBrun (1969), as her $n = 1$ case XIII.4. Regardless of which ODE one integrates, one finds (with C a constant of integration) the general solution

$$t(\tau) = \wp(\tau;\, g_2, g_3) + C, \tag{3.31a}$$

$$g_2 = 4(3C^2 + 1), \qquad g_3 = 8C(C^2 - 1), \tag{3.31b}$$

where τ can be replaced by $A\tau + B$. By substituting into (3.30) and using the identity $\ddot{\wp} = 6\wp^2 - g_2/2$ one obtains the general solution $x = x(\tau)$:

$$(x_1, x_2, x_3)(\tau) = \left(\frac{\dot{\wp}}{\wp + C + 1}, \frac{\dot{\wp}}{\wp + C - 1}, \frac{2\left[(\wp + C)^2 - 1\right]}{\dot{\wp}}\right), \tag{3.32}$$

where τ can be replaced by $A\tau + B$, with x scaled by A. This being meromorphic on the τ-plane, the $\alpha = \beta = -1$ May–Leonard system has the Painlevé property.

That this system can be integrated using elliptic functions was noted by Brenig (1988), but the explicit solution (3.32) is new. It is easily checked that the functions $x_1(x_2 - 2x_3)$, $x_2(x_1 - 2x_3)$ and $x_3(x_1 - x_2)$ are first integrals: they are time-independent, depending only on C and A. They are essentially the first integrals introduced as I_1, I_2, I_3 in (1.9) above (where x is to be read as y). Starting from (3.32), one can confirm that the first integrals found by Llibre & Valls (2011) and Tudoran & Gîrban (2012) are also time-independent.

For the general solution $x=x(\tau)$ of a version of the $\alpha=\beta=-1$ May–Leonard system with a single nonzero growth rate, see example 4.1 below.

4. Unequal growth rates and Painlevé transcendents

Section 3 treated $d=3$ Lotka–Volterra systems classified as 'case II$_i$' according to table 2, with zero growth rates. (The extension to nonzero but equal growth rates is easy, as was noted.) Several $d=3$ systems with unequal growth rates, which have the Painlevé property, will now be completely integrated. They are deformations of systems treated in § 3 but do not fit into the framework of table 2. This is because their first integrals, based on Darboux polynomials, are not conserved: they depend exponentially on τ. Their solutions $x=x(\tau)$ turn out to involve Painlevé transcendents, which for Lotka–Volterra systems is a novelty.

Consider the system

$$\begin{cases} \dot{x}_1 = x_1\left[-a_1x_1 + (1-a_2)x_2 + x_3\right], \\ \dot{x}_2 = x_2\left[+(1-a_1)x_1 - a_2x_2 + x_3\right], \\ \dot{x}_3 = x_3\left[\lambda + (b_1-a_1)x_1 + (b_2-a_2)x_2 - x_3\right], \end{cases} \tag{4.1}$$

which is the $n=1$ specialization of the case-II$_3$ system (3.2), modified to include a growth rate λ for species 3. Up to scaling, this is the generic system in which species 1,2 have equal effects on species 3, species 3 has an equal but negative effect on itself, and species 1,2 have zero growth rates. As in §§ 2 and 3, define an auxiliary variable t by $t=(x_1+x_2)/(x_2-x_1)$. By calculus one deduces that

$$(x_1,x_2,x_3)\,(\tau) = \left(\tfrac{\dot{t}}{t+1},\ \tfrac{\dot{t}}{t-1},\ \tfrac{\ddot{t}}{\dot{t}} - (1-a_1)\tfrac{\dot{t}}{t+1} - (1-a_2)\tfrac{\dot{t}}{t-1}\right)(\tau), \tag{4.2}$$

which previously appeared as Eq. (3.10b).

The new time $t=t(\tau)$ satisfies an extended version of the generalized Schwarzian equation (3.6). If the left side of (3.6) is abbreviated as gS$(a_1,a_2;$ $b_1,b_2;n)$, by tedious elimination one deduces that

$$\mathrm{gS}(a_1,a_2;b_1,b_2;1) + \lambda\left[\left(\frac{1-a_1}{t+1} + \frac{1-a_2}{t-1}\right)\frac{1}{\dot{t}} - \frac{1}{\dot{t}^3}\right] = 0. \tag{4.3}$$

It is straightforward to rewrite this nonlinear third-order ODE in the form $\dot{J}-\lambda J=0$, where

$$J := \frac{\ddot{t} - \left(\frac{1-a_1}{t+1} + \frac{1-a_2}{t-1}\right)\dot{t}^2}{(t+1)^{1-2a_1+b_1}(t-1)^{1-2a_2+b_2}} \tag{4.4}$$

can be viewed as a time-dependent first integral. The existence of such a representation is unsurprising: by exploiting (4.2), one can see that J is the familiar DP-based first integral (3.3) of § 3, written in terms of $t,\dot{t},\ddot{t}$ (and with absolute value signs omitted, so that in general, branch choices must be made).

To deal with the exponential dependence on τ, introduce a new independent variable $z := \mathrm{e}^{\lambda\tau/c}$ for some $c\neq 0$, and denote $\mathrm{d}/\mathrm{d}z$ by a prime. The statement

$J = J_0 e^{\lambda\tau}$ can be written as a nonlinear second-order ODE for $t = t(z)$, i.e.

$$t'' = \left(\frac{1-a_1}{t+1} + \frac{1-a_2}{t-1}\right)(t')^2 - \frac{t'}{z} + K\,\frac{(t+1)^{1-2a_1+b_1}(t-1)^{1-2a_2+b_2}}{z^{2-c}}, \tag{4.5}$$

where $K = c^2 J_0/\lambda^2$ is a constant of integration. Equation (4.5) is a 'proto-Painlevé' ODE, in that for certain $a_1, a_2; b_1, b_2; c$, it defines a Painlevé transcendent (Ince 1927). This is obscured by its singular points being $t = -1, \infty, +1$, while the defining ODE's for the transcendents (traditional; due to Painlevé and Gambier) have singular points $w = 0, 1, \infty$. An equivalent ODE is

$$w'' = \left(\frac{1-a_1}{w} + \frac{1-a_3}{w-1}\right)(w')^2 - \frac{w'}{z} - K\,\frac{w^{1-2a_1+b_1}[(w-1)/2]^{1-2a_3+b_3}}{z^{2-c}}, \tag{4.6}$$

where $w = (t+1)/(t-1) = x_2/x_1$ is a new dependent variable, with $t = (w+1)/(w-1)$; and by definition $a_3 := 1 - a_1 - a_2$ and $b_3 := 1 - b_1 - b_2$.

Example 4.1. For certain $(a_1, a_2; b_1, b_2; c)$, the ODE (4.6) for $w = w(z)$ is or is reducible to a Painlevé-III or Painlevé-V equation. The $\mathrm{P_{III}}$ and $\mathrm{P_V}$ equations have parameters $\alpha, \beta, \gamma, \delta$; and for $\mathrm{N} = \mathrm{III}$ or V, $w_{\mathrm{N}}(z) = w_{\mathrm{N}}(\alpha, \beta, \gamma, \delta; z)$ will denote any solution of the respective equation. The possibilities include

$$\begin{aligned}
(a_1, a_2;\ b_1, b_2;\ c) &= (0, 0;\ \tfrac{2}{r}, -\tfrac{2}{r};\ 2) &:&\quad w = w_{\mathrm{III}}(0, 0, K', 0;\ z)^r,\\
&= (0, 0;\ -\tfrac{2}{3}, -\tfrac{1}{3};\ \tfrac{4}{3}) &:&\quad w = z^{-1} w_{\mathrm{III}}(K', 0, 0, -K';\ z)^3,\\
&= (0, 0;\ -\tfrac{1}{2}, -\tfrac{1}{2};\ 1) &:&\quad w = w_{\mathrm{III}}(K', K', 0, 0;\ z)^2,\\
&= (0, \tfrac{1}{2};\ -\tfrac{1}{2}, 1;\ 1) &:&\quad w = R[w_{\mathrm{III}}(K', K', 0, 0;\ z)^2],\\
&= (\tfrac{1}{2}, \tfrac{1}{2};\ 1, 1;\ 1) &:&\quad w = w_{\mathrm{V}}(0, 0, K', 0; z),
\end{aligned}$$

where $r \neq 0$ is arbitrary, $R[w] := -4w/(w-1)^2$; and $K' \propto K$ is free in each case. These are Carton-LeBrun's $n = 1$ cases e.IV, XI.1, XIII.1, XIII.3, XIII.4. By substituting $t = (w+1)/(w-1)$ into (4.2), one obtains (x_1, x_2, x_3) in terms of the transcendent $w_{\mathrm{N}}(z = e^{\lambda\tau/c})$ and its derivatives.

It should be noted that the last of these complete integrations, in terms of w_{V}, is of a deformed ($\lambda \neq 0$) version of the $\alpha = \beta = -1$ May–Leonard system, which was solved (with $\lambda = 0$) in example 3.7.

The preceding was stimulated by later (1970) results of Carton-LeBrun, who studied and integrated many gSE's of an extended type that includes Eq. (4.3).

5. Summary and final remarks

We have shown [in Eq. (3.10)] how to construct the general solution $x = x(\tau)$ of any $d = 3$ Lotka–Volterra system in which species j, k have equal effects on species i, and the three species have equal growth rates. Such systems had not previously been integrated, despite extensive work. The constructed solution is parametric, with τ, x expressed with the aid of the incomplete beta function as functions of the new time variable $t := (x_j + x_k)/(x_k - x_j)$. If the system has the

Painlevé property, the new time is typically not needed: as a function of τ, the system state x can be expressed in terms of elementary or elliptic functions.

From the complete integration of any Lotka–Volterra system of this type, one can derive first integrals. One is the DP-based first integral of (1.4), the constancy of which defines type II_i. An additional first integral involving a quadrature was found in the ABC case by Goriely (1992), and more generally by Gao (2000, theorem 5). But they did not construct general solutions. It seems difficult to go from a pair of first integrals to a general solution, rather than the reverse.

The fully symmetric ($\alpha=\beta$) May–Leonard model was integrated, and the $\alpha=\beta=-1$ case was treated in examples 3.7 and 4.1. If the growth rates are equal, x is expressed in terms of the Weierstrassian elliptic function $\wp(\tau)$; and if a single rate (λ) is nonzero, the Painlevé transcendent $w_{\mathrm{V}}(\mathrm{e}^{\lambda\tau})$. This case, with equal growth rates, was studied geometrically by Tudoran & Gîrban (2012), but the elliptic general solution is new. The appearance of a Painlevé function is also novel.

The results of Carton-LeBrun (1969, 1970) on certain nonlinear third-order ODE's with the Painlevé property proved invaluable. They are not well known, though they have been re-worked by Cosgrove (1997, Appendix C). In many of our examples they facilitated the integration of the ODE satisfied by the new time $t=t(\tau)$. With further effort, they could probably be made to yield a classification of all type-II_i Lotka–Volterra systems with the Painlevé property.

Our techniques may be useful in constructing solutions of other small-d quadratic dynamical systems, of the sort reviewed in the introduction. A related inverse problem is also of interest. Many functions of time τ have Lotka–Volterra representations, i.e., can be generated from solutions $x=x(\tau)$ of systems of Lotka–Volterra type. (This is stressed by Peschel & Mende (1986), who even mention hardware implementations.) Painlevé functions are included, as § 4 made clear. Along this line, the quadratic representability of solutions of further higher-order ODE's of Painlevé type, such as Chazy equations, will be explored elsewhere.

Appendix: Incomplete beta functions and their inverses

In a normalization used here, the incomplete beta function $\mathrm{B}_{a_1,a_2;t_0}(t)$, for (real) indices a_1,a_2, (real) endpoints $-1,1$ and a (real) basepoint $t_0\neq-1,1$, is given by

$$\mathrm{B}_{a_1,a_2;t_0}(t):=\int_{t_0}^{t}|t'+1|^{a_1-1}\,|t'-1|^{a_2-1}\,dt'. \tag{A.1}$$

The basepoint t_0 lies in one of the intervals $(-\infty,-1)$, $(-1,1)$, $(1,\infty)$, and by convention $\tau=\mathrm{B}_{a_1,a_2;t_0}(t)$ is defined only for t in that interval. It is an increasing function of t. If a_1,a_2 are positive integers it is a polynomial function; and if a_1,a_2 are integers with $a_1a_2<0$ and $a_1+a_2\leqslant 0$, it is a rational function. In general it is a 'special' (higher transcendental) function. If $a_1,a_2>0$ it can be expressed in terms of the traditionally normalized incomplete beta function, which is

$$\mathrm{B}_{\hat t}(a_1,a_2)=\int_0^{\hat t}t^{a_1-1}(1-t)^{a_2-1}\,dt \tag{A.2}$$

for $\hat{t} \in (0,1)$. Specifically,

$$2^{1-a_1-a_2}\,\mathrm{B}_{a_1,a_2;t_0}(t) = \begin{cases} \mathrm{B}_{(t+1)/(t-1)}\,(a_1, 1-a_1-a_2) + C, & t_0 \in (-\infty,-1), \\ \mathrm{B}_{(t+1)/2}\,(a_1,a_2) + C, & t_0 \in (-1,1), \\ \mathrm{B}_{(t-1)/(t+1)}\,(a_2, 1-a_1-a_2) + C, & t_0 \in (1,\infty), \end{cases} \tag{A.3}$$

with $C = C_{a_1,a_2;t_0}$ chosen so that $\mathrm{B}_{a_1,a_2;t_0}(t_0) = 0$. The traditional function $\mathrm{B}_{\hat{t}}(a_1,a_2)$ is supported by many software packages, and many identities, expansions and approximations for it are known (Dutka 1981). In particular,

$$\mathrm{B}_{\hat{t}}(a_1,a_2) = a_1^{-1}\,\hat{t}^{a_1}(1-\hat{t})^{a_2}\,{}_2F_1(a_1+a_2,1;\,a_1+1;\,\hat{t}), \tag{A.4}$$

where ${}_2F_1$ is the Gauss hypergeometric function. Thus for many choices of a_1, a_2, closed-form expressions exist (Prudnikov et al. 1990, § 7.3). A few have been derived in the context of hyperlogistic population growth (Blumberg 1968).

The *inverse* incomplete beta function $t = \mathrm{B}^{-1}_{a_1,a_2;t_0}(\tau)$ is also an increasing function of its argument, and is algebraic if a_1, a_2 are positive integers, or integers with $a_1 a_2 < 0$ and $a_1 + a_2 \leqslant 0$. This inverse function is defined on some interval containing $\tau = 0$, and satisfies (with $\dot{t} = \mathrm{d}t/\mathrm{d}\tau$) the hyperlogistic growth equation

$$\dot{t} = |t+1|^{1-a_1}|t-1|^{1-a_2}, \tag{A.5}$$

with the initial condition $t(\tau = 0) = B^{-1}_{a_1,a_2;t_0}(0) = t_0$. It maps the τ-interval onto whichever of $(-\infty,-1)$, $(-1,1)$, $(1,\infty)$ contains t_0. It is useful to write

$$\mathrm{B}^{-1}_{a_1,a_2;t_0}(\tau) = \mathrm{B}^{-1}_{a_1,a_2}(\tau - \tau_0), \tag{A.6}$$

where $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ is any convenient, standardized solution of (A.5) that maps *some* τ-interval $(\tau_{\min}, \tau_{\max})$ onto the t-interval containing t_0. The time-origin τ_0 is determined by the condition that $\mathrm{B}^{-1}_{a_1,a_2}(-\tau_0) = t_0$.

The function $\tau = \mathrm{B}_{a_1,a_2;t_0}(t)$ can be continued analytically from its real interval of definition to the upper half of the complex t-plane. (The continuation is given by (A.1) without absolute value signs, multiplied by an overall phase factor.) The continuation is a Schwarzian triangle function (Nehari 1952) that performs a Schwarz–Christoffel transformation: provided $a_1, a_2, 1-a_1-a_2$ are non-negative, it conformally maps the upper half of the complex t-plane to the interior of some triangle ΔABC in the τ-plane with vertex angles $\pi(a_1, a_2, 1-a_1-a_2)$, the points $-1, 1, \infty$ on the real t-axis being taken to the vertices A, B, C. Many conformal mapping functions of this type, which are essentially incomplete beta functions, can be found in the catalogue of von Koppenfels & Stallmann (1959). In each case the inverse function takes the interior of ΔABC to the upper-half t-plane.

This inverse $t = \mathrm{B}^{-1}_{a_1,a_2;t_0}(\tau)$ can sometimes be given in closed form; e.g., when the unordered set $\{1/a_1, 1/a_2, 1/(1-a_1-a_2)\}$ is any of $\{2,4,4\}$, $\{2,3,6\}$ or $\{3,3,3\}$. In these cases the inverse can be continued to the entire complex τ-plane from its real interval of definition, and furthermore from ΔABC, by applying the Schwarz reflection principle: reflecting repeatedly through the sides of the triangle. The resulting one-valued function of τ is elliptic (i.e. doubly periodic) and can be given explicitly. The cases $\{1, m, -m\}$ (for m any positive integer), $\{1, \infty, \infty\}$ and $\{2, 2, \infty\}$ are similar, but yield inverse functions $t = \mathrm{B}^{-1}_{a_1,a_2;t_0}(\tau)$ that are elementary rather than elliptic.

Table A.1. Five cases when $t = t(\tau) = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ is expressible in closed form and can be extended to a one-valued function on the complex τ-plane.

a	$t = t(\tau) = \mathrm{B}^{-1}_{a,a}(\tau)$,	$\tau \in (\tau_{\min}, \tau_{\max})$		
	$t_0 \in (-1,1)$ subcase		$\pm t_0 \in (1,\infty)$ subcase	
0	$\tanh\tau$,	$\tau \in (-\infty,\infty)$	$-\coth\tau$,	$\pm\tau \in (-\infty,0)$
$\frac14$	$\sqrt{2}\,[\mathrm{sn}\,\mathrm{dn}](\tau/\sqrt{2})$,	$\tau \in (-\bar{K}_{1/4}, \bar{K}_{1/4})$	$\pm\frac12[\mathrm{cn}^2 + \mathrm{cn}^{-2}](\tau/2)$,	$\pm\tau \in (0, K_{1/4})$
$\frac13$	$-81\,\dot\wp/[2\,(9\,\wp+1)^2]$,	$\tau \in (-\bar{K}_{1/3}, \bar{K}_{1/3})$	$\pm 1 - 8/(27\,\dot\wp \pm 2)$,	$\pm\tau \in (0, K_{1/3})$
$\frac12$	$\sin\tau$,	$\tau \in (-\pi/2, \pi/2)$	$\pm\cosh\tau$,	$\pm\tau \in (0,\infty)$
1	τ,	$\tau \in (-1,1)$	$\pm 1 + \tau$,	$\pm\tau \in (0,\infty)$

Thus there are many 'conformally distinguished' choices for the unordered set $\{1/a_1, 1/a_2\}$, each of which yields an explicit formula for the inverse function $t = \mathrm{B}^{-1}_{a_1,a_2;t_0}(\tau)$. The elementary cases are $\{1,m\}$, $\{1,-m\}$, $\{m,-m\}$, $\{1,\infty\}$, $\{2,2\}$, $\{2,\infty\}$, $\{\infty,\infty\}$, and the elliptic ones are $\{2,3\}$, $\{2,4\}$, $\{2,6\}$, $\{3,3\}$, $\{3,6\}$, $\{4,4\}$. In each of these cases any standardized inverse function $t = \mathrm{B}^{-1}_{a_1,a_2}(\tau)$ of the type used in (A.6), which has a real interval of definition $(\tau_{\min}, \tau_{\max})$, can optionally be continued to a one-valued function on the τ-plane.

Table A.1 gives such a standardized function $t = t(\tau) = \mathrm{B}^{-1}_{a,a}(\tau)$ for $a = 0, \frac14, \frac13, \frac12, 1$. These are the conformally distinguished cases with $a_1 = a_2 =: a$, and are of particular interest (the ones with $a_1 \neq a_2$ are left to the reader). In each case there are two subcases: $t_0 \in (-1,1)$ and $\pm t_0 \in (1,\infty)$. The function $t = t(\tau)$ maps $\tau \in (\tau_{\min}, \tau_{\max})$ onto $t \in (-1,1)$, resp. $\pm t \in (1,\infty)$, and by (A.5) it satisfies

$$\dot t = (1-t^2)^{1-a}, \qquad \text{resp.} \qquad \dot t = (t^2-1)^{1-a}. \tag{A.7}$$

In the table each $t = t(\tau)$ has been chosen to satisfy $t(\tau=0) = 0$, resp. $t(\tau=0) = \pm 1$ (except when $a = 0$). Each is increasing on its interval of definition $(\tau_{\min}, \tau_{\max})$.

The elementary functions appearing in the table (for $a = 0, \frac12, 1$) follow by inspection: by integrating the ODE's (A.7). The elliptic solutions of these ODE's (for $a = \frac14, \frac13$) are less obvious, but can readily be derived with the aid of elliptic function identities from functions that are known to map certain triangles conformally to the upper half-plane (Kober 1957; Sansone & Gerretsen 1969). For $a = \frac14$ the Jacobian elliptic functions $\mathrm{sn}, \mathrm{cn}, \mathrm{dn}$ that appear are 'lemniscatic': their common modular parameter $m = k^2$ equals $\frac12$. For $a = \frac13$ the Weierstrassian elliptic function $\wp(\tau) = \wp(\tau; g_2, g_3)$ that appears is 'equianharmonic': its parameter g_2 equals zero. Also, its parameter g_3 equals $-4/3^6 = -4/729$. It satisfies the usual Weierstrassian ODE $\dot\wp^2 = 4\wp^3 - g_2\wp - g_3$, i.e., $\dot\wp^2 = 4(\wp^3 + 3^{-6})$.

For each function $t = t(\tau) = \mathrm{B}^{-1}_{a,a}(\tau)$ appearing in the table, the interval of definition $\tau \in (\tau_{\min}, \tau_{\max})$ is easily computed from (A.1). It can be expressed in terms of the traditionally normalized *complete* beta function $\mathrm{B}(a_1, a_2) := \Gamma(a_1)\Gamma(a_2)/\,\Gamma(a_1+a_2)$. In the subcases $t_0 \in (-1,1)$ and $\pm t_0 \in (1,\infty)$, it is

$$\tau \in (-\bar{K}_a, \bar{K}_a), \qquad \text{resp.} \qquad \pm\,\tau \in (0, K_a), \tag{A.8}$$

where

$$\bar{K}_a := \tfrac{1}{2}\,\mathrm{B}(a,\tfrac{1}{2}) = \frac{1}{2}\,\frac{\Gamma(a)\,\Gamma(\frac{1}{2})}{\Gamma(a+\frac{1}{2})}, \quad \text{resp.} \quad K_a := \tfrac{1}{2}\,\mathrm{B}(a,\tfrac{1}{2}-a) = \frac{1}{2}\,\frac{\Gamma(a)\,\Gamma(\frac{1}{2}-a)}{\Gamma(\frac{1}{2})}.$$

It is understood that $\bar{K}_a$ is infinite if $a \leqslant 0$. For instance, $\bar{K}_0, \bar{K}_{1/2}, \bar{K}_1$ are $\infty, \pi/2, 1$, as shown. Also, in the $\pm t_0 \in (1,\infty)$ case the interval $\pm\tau \in (0, K_a)$ must be replaced by $\pm\tau \in (-\infty, 0)$ if $a \leqslant 0$, and interpreted as $\pm\tau \in (0,\infty)$ if $a \geqslant \frac{1}{2}$.

The values of a in the table are not the only ones for which the inverse function $t = t(\tau) = \mathrm{B}_{a,a}^{-1}(\tau)$ can be expressed in closed form. It is an algebraic function if a is any positive integer, and if $a = 2$ it can even be expressed in terms of radicals. But for any integer $a > 1$, its continuation to the τ-plane is multiple-valued.

No similar table of closed-form expressions seems to have appeared previously; though certain values of the traditionally normalized inverse incomplete beta function (especially for large (half-)integral values of a_1, a_2) were calculated and tabulated long ago, owing to their importance in statistics (Thompson 1941).

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